

PHYSIOLOGICAL ECOLOGY OF INCUBATION IN TROPICAL SEABIRDS

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ABSTRACT.—Loss of water vapor and carbon dioxide from the egg, uptake of oxygen, and transfer of heat to the egg were compared in tropical seabirds and seabirds breeding in higher latitudes. In the smaller Procellariiformes (petrels, shearwaters) the rate of gas transfer (water vapor, carbon dioxide and oxygen) across the eggshell was relatively low, regardless of geographical distribution. Gas transfer was also comparatively low in tropical charadriiform and pelecaniiform seabirds that have been studied. To a large extent, these low rates of gas transfer could be attributed to prolonged incubation which is a feature of the smaller Procellariiformes and of tropical seabirds in general. Gas transfer between eggs and their environment is greatly influenced by the sequence of events during pipping. In many tropical seabirds a relatively large percentage of total water loss from, and oxygen uptake by, the egg, occurs during the pipping phase. Heat transfer between parent bird and the egg is poorly understood in seabirds and there is a need to standardize the measurement of egg temperature so that valid comparisons may be made between species.

Physiological ecology deals with the exchange of materials and energy between an organism and its natural environment. In the specific instance of the seabird's egg, the only such exchanges that occur are the loss of water vapor and carbon dioxide from the egg to the environment, the uptake of oxygen by the egg, and the transfer of heat from the incubating adult to the egg. These exchanges are determined partly by the size and structure of the egg, partly by the physiological activity and growth of the embryo, and partly by ecological factors. Many of these factors are interrelated. The purpose of this paper is to summarize what is known about the factors that affect gas and heat transfer between the egg and its microclimate. Special attention is given to differences between tropical seabirds and seabirds of higher latitudes.

There is no satisfactory definition of a "tropical seabird." For the present review, Ashmole's (1971) definition of the tropic zone was adopted—"comprising all areas where the sea-surface temperature remains above 23°C throughout the year. This approximates the area enclosed by the 23° isotherms for February and August in the Northern and Southern hemispheres, respectively." Thus, all seabirds nesting within a geographical area confined by the 23°C isotherms have been designated tropical seabirds. Seabirds nesting outside this zone were considered to be from "higher latitudes." This definition is less arbitrary than the rigid exclusion of species nesting outside the Tropics of Cancer and Capricorn, and considerably less confining than the use of the tropical convergence (where warm and cool ocean currents meet) to delineate boundaries.

In some instances, insufficient data were available to allow comparisons between tropical sea-

birds and those that breed in higher latitudes. For the same reason little attempt has been made to distinguish between different families of seabirds.

WATER LOSS FROM THE EGGS

DAILY RATE OF WATER LOSS (\dot{M}_{H_2O})

The mass of the avian egg decreases continuously throughout incubation. This is largely due to loss of water from the egg (Drent 1973, Rahn and Ar 1974). For birds in general, the daily water loss from the egg (\dot{M}_{H_2O}) may be predicted from the mass of the freshly-laid egg by means of the following relationship:

$$\dot{M}_{H_2O} = 13.243 W^{0.754} \quad (\text{Ar and Rahn 1980})$$

(mg/day) (g)

in which \dot{M}_{H_2O} = daily mass loss in mg/day, W = mass of the freshly laid egg in g. This relationship is represented in Figures 1 and 2 by the solid line. All Procellariiformes were below the line, indicating that the water loss from their eggs was less than expected, on the basis of fresh-egg mass (Fig. 1). Insufficient data were available to permit comparisons between tropical seabirds and other seabirds within the order Procellariiformes. The magnitude of the deviation from predicted values, based on egg mass, seemed to be greater for the smaller species. However, the lowest values were for the Fork-tailed Storm-Petrel, *Oceanodroma furcata*, a species which deserts its egg for part of the time, a circumstance which would result in a reduced water loss from the egg. The smallest deviation from predicted values was recorded from the Dark-rumped Petrel, *Pterodroma phaeopygia*, which nests at 3000 m in Haleakala Crater on Maui in the Hawaiian Islands. At this altitude enhanced water loss from the egg is a serious problem because of the reduced barometric pressure (Carey 1980).

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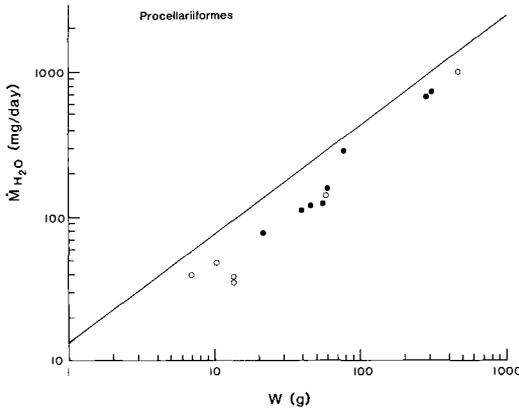


FIGURE 1. Relationship between daily rate of water loss from eggs (\dot{M}_{H_2O}) and fresh-egg mass (W) in the Procellariiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $\dot{M}_{H_2O} = 13.243 W^{0.754}$ (Ar and Rahn 1980). Data from Harris (1966), Tickell (1968), Scott (1970), Boersma and Wheelwright (1979), Grant et al. (1982a, b), Whittow et al. (1982), Rahn and Huntington, pers. comm.; Grant, Whittow and Pettit, unpubl. data, Simons and Whittow, unpubl. data, Whittow, Garnett and Teebaki, unpubl. data, Whittow and Pettit, unpubl. data.

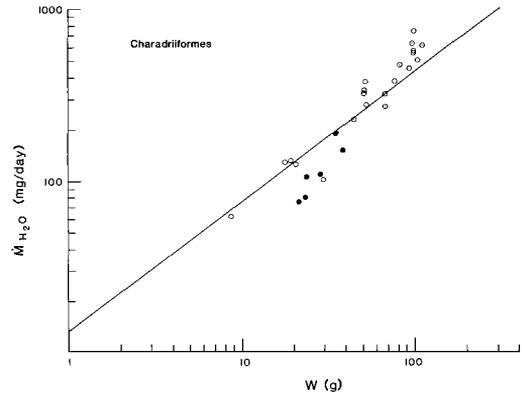


FIGURE 2. Relationship between daily rate of water loss from eggs (\dot{M}_{H_2O}) and fresh-egg mass (W) in the Charadriiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $\dot{M}_{H_2O} = 13.243 W^{0.754}$ (Ar and Rahn 1980). Data from Drent (1970), Rahn et al. (1976), Rahn et al. (1977), Morgan et al. (1978), Rahn and Dawson (1979), Roudybush et al. (1980), Pettit et al. (1981), Vleck, Vleck, Rahn and Paganelli, pers. comm., Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

Among the Charadriiformes also, the water loss from the eggs of the tropical species (terns and noddies) was less than predicted values based on fresh-egg mass (Fig. 2). The daily water loss from the eggs of species from higher latitudes, on the other hand, was close to, or higher than, predicted values. There were two exceptions to this generalization: the water loss from the eggs of the Sooty Tern, *Sterna fuscata*, a tropical species, was very close to the expected value, while that from the Cassin's Auklet's, *Ptychoramphus aleuticus*, egg was considerably lower than predicted.

Insufficient data were available for the water loss from eggs of Pelecaniformes breeding in higher latitudes to permit comparisons with tropical species. However, Table 1 reveals that the values for \dot{M}_{H_2O} in four tropical species were all below the values predicted on the basis of the fresh-egg mass.

Water-vapor conductance of the shell (G_{H_2O})

The rate of water loss from the egg is determined by the water-vapor conductance of the shell (G_{H_2O}) on the one hand, and the difference in water-vapor pressure across the shell (ΔP_{H_2O}), on the other:

TABLE 1
WATER LOSS (\dot{M}_{H_2O}) FROM THE EGGS OF FOUR TROPICAL PELECANIFORMES

Species	W (g) ^a	\dot{M}_{H_2O} (mg/day)		Reference
		Measured	Predicted ^b	
White-tailed Tropicbird (<i>Phaethon lepturus</i>)	40.7	170.0	216.6	Stonehouse 1962, 1963
Red-footed Booby (<i>Sula sula</i>)	58.3	167.1	284.0	Whittow and Pettit, unpubl. data.
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	71.6	199.2	331.6	Whittow, Grant and Pettit, unpubl. data
Great Frigatebird (<i>Fregata minor</i>)	89.1	194.3	391.0	Grant, Whittow and Pettit, unpubl. data

^a W = Fresh-egg mass.

^b $\dot{M}_{H_2O} = 13.243 W^{0.754}$ (Ar and Rahn 1980).

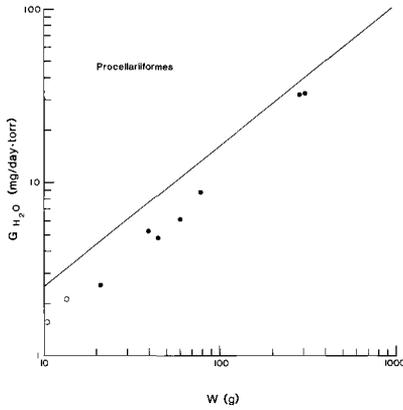


FIGURE 3. Relationship between water-vapor conductance of egg shells and shell membranes (G_{H_2O}) and the fresh-egg mass (W) in Procellariiformes. ● = tropical species; ○ = species breeding in higher latitudes. The solid line represents the relationship $G_{H_2O} = 0.384 W^{0.814}$ (Ar and Rahn 1978). Data from Vleck and Kenagy (1980), Grant et al. 1982a, b, Whittow et al. 1982, Rahn and Huntington, pers. comm., Grant, Whittow and Pettit, unpubl. data, Pettit and Whittow, unpubl. data, Whittow and Simons, unpubl. data.

$$\dot{M}_{H_2O} = \frac{G_{H_2O}}{(\text{mg/day})} \cdot \frac{\Delta P_{H_2O}}{(\text{torr})} \quad (\text{Rahn and Ar 1974})$$

The water-vapor conductance is a measure of the rate at which water vapor may diffuse through the shell and shell membranes. The water-vapor conductance is related to egg mass as follows:

$$G_{H_2O} = 0.384 W^{0.814} \quad (\text{g/day torr}) \quad (\text{g}) \quad (\text{Ar and Rahn 1978})$$

represented by the solid line in Figures 3 and 4. The water-vapor conductance of the eggs of Procellariiformes was lower than predicted values based on egg mass, but it was not possible to distinguish between tropical and non-tropical species (Fig. 3). As was true for water loss from eggs (Fig. 1), values for the two largest species were closer to the expected values than were values for smaller eggs. As far as Charadriiformes are concerned, species from higher latitudes were well represented by predictions based on their egg mass (Fig. 4); Cassin's Auklet presented the greatest deviation. Among tropical species the deviation was least in the Sooty Tern and greatest in the White Tern, *Gygis alba*. The available data on water-vapor conductance of eggs of Pelecaniformes are presented in Table 2. All measured values were lower than expected in tropical species. They were lower in the two species from

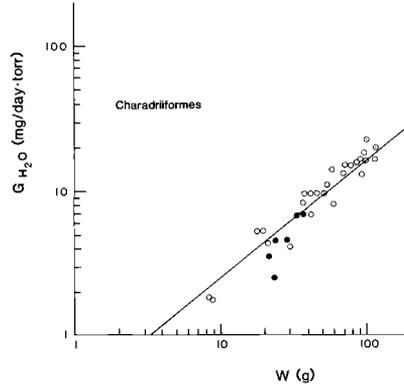


FIGURE 4. Relationship between water-vapor conductance of egg shells and shell membranes (G_{H_2O}) and fresh-egg mass (W) in Charadriiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $G_{H_2O} = 0.384 W^{0.814}$ (Ar and Rahn 1980). Data from Ar et al. (1974), Rahn et al. (1976), Ar and Rahn (1978), Morgan et al. (1978), Rahn and Dawson (1979), Roudybush et al. (1980), Pettit et al. (1981), Grant, Whittow and Pettit, unpubl. data, Vleck, Vleck, Rahn and Paganelli, pers. comm.

higher latitudes also, but clearly more information is needed on non-tropical species, particularly in view of the discrepancy between the two sets of values for the Double-crested Cormorant, *Phalacrocorax auritus*.

Shell thickness (L).—One factor determining the water-vapor conductance of the shell is the shell thickness, because thickness largely prescribes the length of the pathway along which water vapor must diffuse. Shell thickness (L) may also be predicted from mass (W) of the freshly laid egg:

$$L = 5.126 \cdot 10^{-2} W^{0.456} \quad (\text{mm}) \quad (\text{g}) \quad (\text{Ar et al. 1974})$$

This relationship is represented by the solid line in Figure 5, which presents data for shell thickness of Procellariiformes. All procellariiform shells were thinner than expected but there seemed to be little difference between the tropical species and other seabirds in this connection. Therefore, low water-vapor conductance of the shell (Fig. 3) was not the consequence of a thicker shell. The shells of charadriiform seabirds were also thinner than for birds in general (Fig. 6) but there seemed to be little difference between tropical and non-tropical species (Fig. 6). What little information exists on the Pelecaniformes suggests that species with obviously chalky shell surfaces (cormorants, boobies) have thicker shells than might be expected on the basis of their fresh-

TABLE 2
WATER-VAPOR CONDUCTANCE (G_{H_2O}) OF THE EGG SHELL AND SHELL MEMBRANES OF PELECANIFORM SEABIRDS

Species	W (g) ^a	G_{H_2O} (mg/day torr)		Reference
		Measured	Predicted ^b	
Tropical species				
Red-footed Booby (<i>Sula sula</i>)	58.3	5.80	10.51	Whittow, Pettit, Ackerman and Paganelli, unpubl. data
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	67.7	9.56	11.88	Ar and Rahn 1978
	71.6	8.98	12.42	Grant, Whittow and Pettit, unpubl. data
Brown Booby (<i>Sula leucogaster</i>)	67.8	7.64	11.88	Ar and Rahn 1978
Great Frigatebird (<i>Fregata minor</i>)	89.1	7.50	14.84	Grant, Whittow and Pettit, unpubl. data
Species breeding in higher latitudes				
Pelagic Cormorant (<i>Phalacrocorax pelagicus</i>)	39.3	6.78	7.62	Ar and Rahn 1978
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	49.9	5.56	9.26	Ar and Rahn 1974
	57.7	8.36	10.42	Ar and Rahn 1978

^a W = Fresh-egg mass.

^b G_{H_2O} = $0.384 W^{0.814}$ (Ar and Rahn 1978).

egg mass (Table 3). This must be considered as contributory to the low values for G_{H_2O} included in Table 2. The Great Frigatebird, *Fregata minor*, and Red-tailed Tropicbird, *Phaethon rubricauda*, on the other hand, had relatively thin egg shells (Table 3).

Total functional pore area (A_p).—Water vapor diffuses through pores in the shell. The total functional pore area provides an indication of the pore area available for diffusion. Based, in theory, on Fick's Law of Diffusion (Ar et al. 1974), the total functional pore area may be calculated from the measured values of shell thickness (L) and water-vapor conductance (G_{H_2O}):

$$A_p = 0.447 \cdot G_{H_2O} \cdot L$$

(mm²) (mg/torr·day)(mm)
(Rahn et al. 1976)

The functional pore area so calculated is related to the mass of the freshly laid egg, in most birds, as follows:

$$A_p = 9.2 \cdot 10^{-3} \cdot W^{1.236} \quad (\text{Ar et al. 1974})$$

(mm²) (g)

Figure 7 reveals that the functional pore area in Procellariiformes was lower than the value predicted by the above equation, represented in Figure 7, by the solid line. There is no indication from the limited data in Figure 7 that tropical species differed from other seabirds in this respect. In temperate Charadriiformes (Fig. 8) calculated values for A_p were distributed about the line representing predicted values. Tropical

species were all below the line but only the White Tern's egg had a functional pore area significantly below predictions. The two cormorants that made up the sample of Pelecaniformes from higher latitudes both had functional pore areas greater than the predicted value (Table 4). All four tropical species had lower values, that for the Great Frigatebird was particularly low—only 52% of predicted.

Number of pores in the eggshell (N).—A low functional pore area means that there are fewer pores in the shell, pores are of smaller diameter, or both. The number of pores (N) in an egg is related to the mass of the freshly laid egg in the following way:

$$N = 1449 \cdot W^{0.42}$$

(pores/egg) (g)
(Tullet and Board 1977)

This relationship holds for a large number of birds and it is represented by the solid line in Figure 9. The seabirds included in Figure 9 all had fewer pores in their eggshells than might be expected, on the basis of egg mass, with the exception of the two albatross, the largest species included in Figure 9. The pore count for Abbott's Booby, *Sula abbotti*, was also close to the value predicted by the line. Abbott's Booby has the largest egg of any booby and also the longest incubation period in relation to egg mass. Since the pore count included in Figure 9 was performed on a fragment of shell it would seem important to corroborate this datum point on additional specimens of shell.

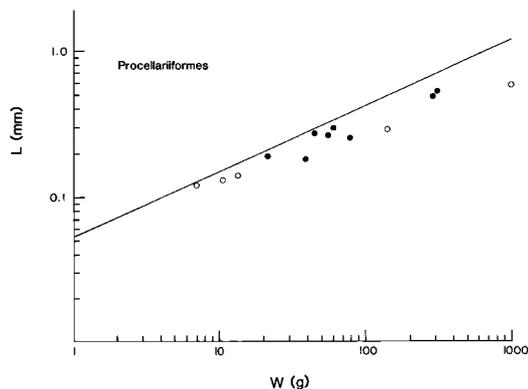


FIGURE 5. Relationship between eggshell thickness (L) and fresh-egg mass (W) in Procellariiformes. ● = tropical species; ○ = breeding in higher latitudes. The line represents the relationship $L = 5.126 \cdot 10^{-2} \cdot W^{0.456}$ (Ar et al. 1974). Data from Harris (1966), Tickell (1968), Scott (1970), Vleck and Kenagy (1980), Grant et al. (1982a, b), Whittow et al. (1982), Rahn and Huntington, pers. comm.; Whittow, Garnett, and Teebaki, unpubl. data, Whittow, Grant, Pettit and Naughton, unpublished data, Whittow, Pettit and Naughton, unpubl. data, Whittow and Simons, unpubl. data.

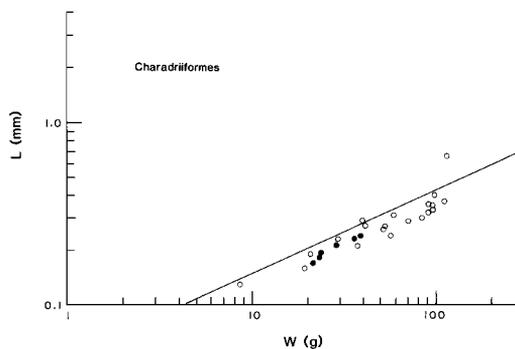


FIGURE 6. Relationship between eggshell thickness (L) and fresh-egg mass (W) in Charadriiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $L = 5.126 \cdot 10^{-2} \cdot W^{0.456}$ (Ar et al. 1974). Data from Rahn et al. (1976), Ar and Rahn (1978), Morgan et al. (1978), Rahn and Dawson (1979), Roudybush et al. (1980), Pettit et al. (1981), Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

In fact, Figure 9 presents evidence that there is a difference in the relationship between pore numbers and fresh-egg mass in seabirds and in the birds represented by the line, rather than be-

tween tropical seabirds and other seabirds. The relationship for seabirds is as follows:

$$N = 278.6 \cdot W^{0.704}$$

Pore geometry.—Functional pore area A_p may be divided by number of pores to obtain the average area for each pore (P_a). The radius (P_r) of a single average pore may then be derived from the relationship:

TABLE 3
EGGSHELL THICKNESS (L) OF PELECANIFORM SEABIRDS

Species	W (g) ^a	L (mm)		Reference
		Meas-ured	Pre-dicted ^b	
Tropical species				
Red-footed Booby (<i>Sula sula</i>)	58.3	0.40	0.33	Whittow, Pettit, Ackerman and Paganelli, unpubl. data
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	67.7	0.36	0.35	Ar and Rahn 1978
	71.6	0.34	0.36	
Brown Booby (<i>Sula leucogaster</i>)	67.8	0.39	0.35	Whittow, Grant and Pettit, unpubl. data
Great Frigatebird (<i>Fregata minor</i>)	89.1	0.37	0.40	Ar and Rahn 1978
Abbott's Booby (<i>Sula abbotti</i>)	112.0	0.48	0.44	Whittow, Grant and Pettit, unpubl. data
				Whittow, Rahn and Powell, unpubl. data; Nelson, 1971
Species breeding in higher latitudes				
Pelagic Cormorant (<i>Phalacrocorax pelagicus</i>)	39.3	0.35	0.27	Ar and Rahn, 1978
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	57.7	0.39	0.33	Ar and Rahn, 1978

^a W = Fresh-egg mass.

^b $L = 5.126 \cdot 10^{-2} \cdot W^{0.456}$ (Ar et al. 1974).

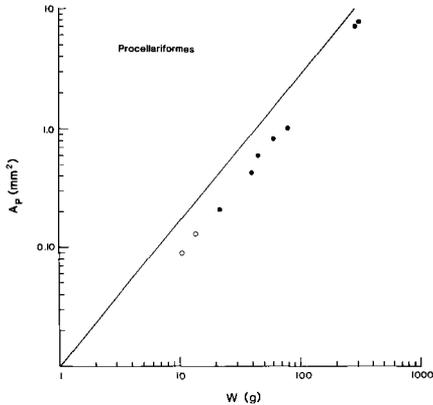


FIGURE 7. Relationship between functional pore area (A_p) of eggshell and fresh-egg mass (W) in Procellariiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $A_p = 9.2 \cdot 10^{-3} \cdot W^{1.236}$ (Ar et al. 1974). Data from Vleck and Kenagy (1980), Grant et al. (1982a, b), Whittow et al. (1982), Rahn and Huntington, pers. comm., Grant, Whittow, Pettit and Naughton, unpubl. data, Whittow and Simons, unpubl. data.

$$P_r = \sqrt{P_A/\pi} \quad (\text{Rahn 1980})$$

Allometric relationships have not been established for pore area and radius. In Figures 10 and 11 available data for P_A and P_r are plotted against mass of the fresh egg, for tropical and non-tropical seabirds. There was a linear relationship between both P_A and P_r on one hand, and W on the other (Figs. 10, 11) and little evidence of any

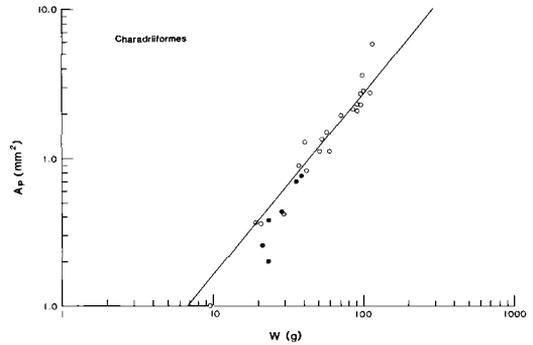


FIGURE 8. Relationship between functional pore area (A_p) of eggshell and fresh-egg mass (W) in Charadriiformes. ● = tropical species; ○ = species breeding in higher latitudes. The line represents the relationship $A_p = 9.2 \cdot 10^{-3} \cdot W^{1.236}$ (Ar et al. 1974). Data from Rahn et al. (1976), Ar and Rahn (1978), Morgan et al. (1978), Rahn and Dawson (1979), Roudybush et al. (1980), Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

difference between tropical seabirds and other birds.

Water-vapor pressure difference (ΔP_{H_2O})

As indicated above, daily rate of water loss from the egg is determined by two factors: water-vapor conductance of the shell (G_{H_2O}) and the difference in water-vapor pressure (ΔP_{H_2O}) between contents of the egg and the microclimate of the incubated egg. Preceding sections have shown that water-vapor conductance of shells of many seabird eggs, particularly those of tropical

TABLE 4
FUNCTIONAL PORE AREA (A_p) OF THE EGG SHELL OF PELECANIFORM SEABIRDS

Species	W (g) ^a	A_p (mm ²)		Reference
		Calculated ^b	Predicted ^c	
Tropical species				
Red-footed Booby (<i>Sula sula</i>)	58.3	1.04	1.40	Whittow, Pettit, Ackerman and Paganelli, unpubl. data
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	67.7	1.54	1.68	Ar and Rahn 1978
	71.6	1.36	1.80	Whittow, Grant and Pettit, unpubl. data
Brown Booby (<i>Sula leucogaster</i>)	67.8	1.33	1.69	Ar and Rahn 1978
Great Frigatebird (<i>Fregata minor</i>)	89.1	1.24	2.37	Whittow, Grant and Pettit, unpubl. data
Species breeding in higher latitudes				
Pelagic Cormorant (<i>Phalacrocorax pelagicus</i>)	39.3	1.06	0.86	Ar and Rahn 1978
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	57.7	1.46	1.38	Ar and Rahn 1978

^a W = Fresh-egg mass.

^b $A_p = 0.447 \cdot G_{H_2O} \cdot L$. (Rahn et al. 1976).

^c $A_p = 9.2 \cdot 10^{-3} \cdot W^{1.236}$ (Ar et al. 1974).

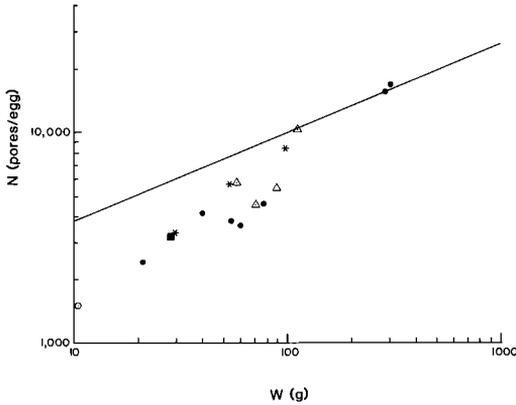


FIGURE 9. Relationship between number of pores (N) in eggshells of sea birds and fresh-egg mass (W). ● = tropical Procellariiformes; ○ = Procellariiformes breeding in higher latitudes; ■ = tropical Charadriiformes; * = Charadriiformes breeding in higher latitudes; Δ = tropical Pelecaniformes. The line represents the relationship $N = 1449 \cdot W^{0.42}$ (Tullet and Board 1977). Data from Nelson (1971), Rahn and Dawson (1979), Roudybush et al. (1980), Grant et al. (1982a, b), Whittow et al (1982), Rahn and Huntington, pers. comm. Whittow and Pettit, unpubl. data, Whittow, Garnett, Teebaki and Pettit, unpubl. data, Whittow, Grant and Pettit, unpubl. data, Whittow, Pettit and Naughton, unpubl. data, Whittow, Simons, and Pettit, unpubl. data, Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

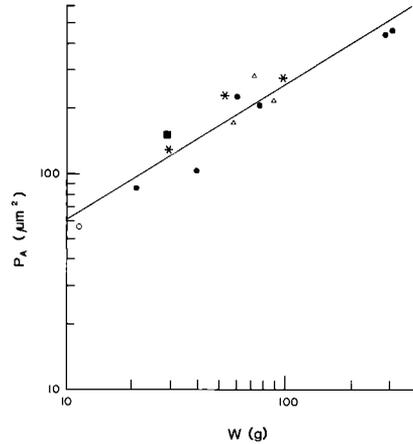


FIGURE 10. Relationship between mean area of a pore (P_A) and fresh-egg mass (W). ● = tropical Procellariiformes; ○ = Procellariiformes breeding in higher latitudes; ■ = tropical Charadriiformes; * = Charadriiformes breeding in higher latitudes; Δ = tropical Pelecaniformes. The line represents the relationship $P_A = 14.44 \cdot W^{0.627}$, $r = 0.954$ (correlation coefficient), calculated as linear regression of logarithms of data. Data from Rahn and Dawson (1979), Roudybush et al. (1980), Grant et al. (1982a, b), Whittow et al. (1982), Rahn and Huntington, pers. comm., Whittow and Pettit, unpubl. data, Whittow, Garnett, Teebaki and Pettit, unpubl. data, Whittow, Grant and Pettit, unpubl. data, Whittow, Simons and Pettit, unpubl. data, Whittow, Grant, Flint, Pettit and Naughton, unpubl. data.

seabirds, is lower than expected. Is there a comparable reduction in ΔP_{H_2O} ? Values for ΔP_{H_2O} may be calculated if \dot{M}_{H_2O} and G_{H_2O} are known. Data for ΔP_{H_2O} , so calculated, are shown in Table 5. Data for Fork-tailed Storm-Petrels are no more than an approximation because of the variable degree of egg neglect in this species. Ar and Rahn (1980) reported an average value of 34 torr for ΔP_{H_2O} in a large number of birds. Table 5 reveals that average values for three orders of seabirds were below this figure. Average values for species breeding more distant from the equator were higher than those of tropical species, but adequate data for statistical comparisons were available only for Charadriiformes. That comparison did not reveal a significant difference between tropical and non-tropical species. Little evidence exists at present that a lower value for ΔP_{H_2O} in tropical seabirds contributes to their relatively low \dot{M}_{H_2O} .

Water-vapor pressure of egg contents ($P_{H_2O,egg}$). — Water-vapor pressure difference ΔP_{H_2O} is the difference between water-vapor pressure of contents of the egg ($P_{H_2O,egg}$) and that of the microclimate of the egg ($P_{H_2O,neest}$). Assuming that contents of the egg are saturated with water vapor, water-vapor pressure may be cal-

culated if egg temperature is known. Mean central egg temperatures (T_{egg}) of seabirds are included in Table 5 together with egg water-vapor

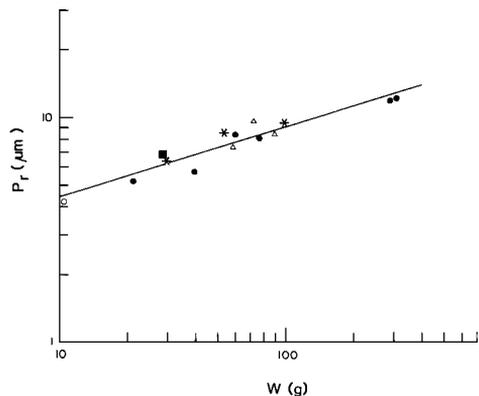


FIGURE 11. Relationship between pore radius (P_r) and fresh-egg mass (W). The symbols and sources of data are the same as in Figure 10. The line represents the relationship $P_r = 2.17 \cdot W^{0.31}$, $r = 0.947$ (correlation coefficient), calculated as linear regression of logarithms of data.

pressures ($P_{H_2O,egg}$) derived from them. Variations in water-vapor pressure of the egg reflect variations in egg temperature. Mean egg temperature of twenty-seven species of birds was reported to be 35.6°C by Drent (1975). The average values for the seabirds included in Table 5 were close to, or above, 35.6°C. Procellariiform eggs tended to be incubated at a relatively low temperature; the egg temperature of the Fork-tailed Storm-Petrel's egg is particularly low. In some seabirds (e.g., the Laysan Albatross, *Diomedea immutabilis*) it is known that the central egg temperature changes during incubation. A single value for egg temperature may therefore be quite misleading. It would be valuable, for future reference, if egg temperatures were measured at comparable stages in development of the embryo. The time immediately prior to the initial event in the pipping process would be a useful reference point for comparisons between species, and it would also be in accord with measurements of embryonic oxygen consumption and other physiological variables (see below).

The technique of measuring egg temperature is also a source of variation. Insertion of a rapidly responding, fine needle thermistor probe immediately after removal of the egg from under the bird is the method of choice. Indwelling thermistors invariably result in death of the embryo, abolition of embryonic heat production, and a change in egg temperature (Grant et al. 1982b). The position of the tip of the thermistor is also important. From the standpoint of embryonic development and metabolism, the thermistor tip should be placed close to the embryo, which changes position during incubation. If egg temperature is taken immediately prior to the initial event during pipping, as suggested above, the center of the egg would be an appropriate position for the thermistor tip. Central egg temperature would also be the best *single* position for the measurement of egg temperature for calculations of heat transfer between the egg and its surroundings and also for computation of the water-vapor pressure inside the egg.

Water-vapor pressure of the nest ($P_{H_2O, nest}$).— Subtraction of the water-vapor pressure difference (ΔP_{H_2O}) from water-vapor pressure of the contents of the incubated egg ($P_{H_2O,egg}$), yields water-vapor pressure of the micro-climate of the incubated egg ($P_{H_2O, nest}$). This value may also be measured directly, by the technique of egg hygrometry (Rahn et al. 1977). The information in Table 5 was derived from both computed and measured values. Ar and Rahn (1978) reported that the average water-vapor pressure of the egg's micro-climate was 19 torr, for 23 species. Average values for tropical species of seabirds, given in Table 5, were close to this figure (19). How-

ever, mean values do not reveal some interesting divergences from the mean. Thus, among tropical Procellariiformes, the $P_{H_2O, nest}$ for two burrowing species, Bonin Petrel, *Pterodroma hypoleuca*, (Grant et al. 1982a) and Wedge-tailed Shearwater, *Puffinus pacificus* (Whittow et al. 1982), are not notably different from those for the surface nesting Laysan and Black-footed albatross, *Diomedea nigripes* (Grant et al. 1982b), and the Christmas Shearwater, *Puffinus nativitatus* (Whittow, Grant and Pettit, unpub. data). In tropical Pelecaniformes, information was available on only three species. The lowest value (15.8 torr) was recorded in the Red-footed Booby, *Sula sula* (Whittow and Pettit, unpubl. data), a tree-nesting species, and the highest figure occurred in the Red-tailed Tropicbird (Whittow, Grant and Pettit, unpub. data), which lays its egg directly on the moist soil. The two petrels from higher latitudes had especially low values for $P_{H_2O, nest}$; the Fork-tailed Storm-Petrel (Boersma and Wheelwright 1979, Vleck and Kenagy 1980), neglects its egg for a variable amount of time and, during this time, the microclimate of the egg is that of ambient air, i.e., the $P_{H_2O, nest}$ is correspondingly low. However, the low egg temperature of the continuously incubated egg (Table 5) would, other things being equal, lead to a low calculated value for $P_{H_2O, nest}$ in this species. The low water-vapor pressure of the cooler air may also be a factor in determining the low $P_{H_2O, nest}$ in the Fork-tailed and Leach's Storm-Petrel, *Oceanodroma leucorhoa*, (Rahn and Huntington, pers. comm.). The diversity of values among Charadriiformes is considerable.

NEST VENTILATION (\dot{V}_{nest})

Water that diffuses out of the egg into the microclimate of the egg is ultimately lost to ambient air. Water loss from the incubated egg's microclimate to the surrounding air occurs by a combination of diffusion and convection. Convection is probably the major pathway for water loss, especially if there is air movement around the incubating bird. Moreover, convective water loss is susceptible to modification by the incubating bird itself. Thus, each time the bird stands up, turns its egg or leaves the egg unattended, there must be an increased convective water loss from the vicinity of the egg. Rahn et al. (1976) presented an equation to describe this convective water loss in terms of the amount of ventilation ("nest ventilation") required to remove water lost from the egg:

$$\dot{V}_{nest} = \frac{\dot{M}_{H_2O}}{(l/day)} \div \frac{(C_{nest} - C_{air})}{(mg/l)} \quad \text{(Rahn et al. 1976)}$$

where \dot{V}_{nest} = nest ventilation; \dot{M}_{H_2O} = daily water

TABLE 5
 WATER-VAPOR PRESSURE DIFFERENCE (ΔP_{H_2O}) BETWEEN THE EGG AND THE NEST MICROCLIMATE, CENTRAL EGG TEMPERATURE (T_{egg}), WATER-VAPOR PRESSURE INSIDE THE EGG ($P_{H_2O,egg}$) AND IN THE NEST MICROCLIMATE ($P_{H_2O,nest}$). DATA ARE FROM REFERENCES CITED IN FIGURES 1–4 AND TABLES 1–2 UNLESS OTHERWISE INDICATED

Order Breeding latitude Species	ΔP_{H_2O} (torr)	T_{egg} (°C)	$P_{H_2O,egg}$ (torr)	$P_{H_2O,nest}$ (torr)
Procellariiformes				
Tropical				
Bulwer's Petrel (<i>Bulweria bulwerii</i>)	30.3	—	—	—
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	21.3	33.8	39.5	18.1 ^d
Christmas Shearwater (<i>Puffinus nativitatis</i>)	24.8	35.3	42.9	18.1
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	22.6	35.0	42.2	19.6 ^d
Dark-rumped Petrel (<i>Pterodroma phaeopygia</i>)	21.9	34.9	41.9	20.0
Laysan Albatross (<i>Diomedea immutabilis</i>)	25.0	35.8	44.1	19.1 ^d
Black-footed Albatross (<i>Diomedea nigripes</i>)	24.9	35.0	42.2	17.3 ^d
	<u>24.4</u>	<u>35.0</u>	<u>42.1</u>	<u>18.7</u>
Higher latitudes				
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>)	30.7	33.4	38.6	7.9
Fork-tailed Storm-Petrel (<i>Oceanodroma furcata</i>)	16.6	29.7 ^a	31.3	14.7
	<u>23.7</u>	<u>31.6</u>	<u>34.9</u>	<u>11.3</u>
Charadriiformes				
Tropical				
White Tern (<i>Gygis alba</i>)	21.3	35.4	43.1	22.0
	26.8	35.3	42.9	14.6 ^d
	23.5	37.4	48.1	24.5
Black Noddy (<i>Anous tenuirostris</i>)	—	34.9	41.9	—
Sooty Tern (<i>Sterna fuscata</i>)	28.1	35.7 ^b	43.8	15.7
Brown Noddy (<i>Anous stolidus</i>)	25.3	35.6	43.6	18.3
Gray-backed Tern (<i>Sterna lunata</i>)	23.6	36.5	45.8	22.2
	<u>24.8</u>	<u>35.9</u>	<u>44.2</u>	<u>19.4</u>
Higher latitudes				
Least Tern (<i>Sterna albifrons</i>)	35.2	—	—	—
Arctic Tern (<i>Sterna paradisaea</i>)	25.1	—	—	—
Common Tern (<i>Sterna hirundo</i>)	29.3	—	—	—
Forster's Tern (<i>Sterna forsteri</i>)	21.3	34.8	41.7	20.4 ^{d,e}
Cassin's Auklet (<i>Ptychoramphus aleuticus</i>)	24.8	—	—	—
Sandwich Tern (<i>Sterna sandvicensis</i>)	22.0	—	—	—
Laughing Gull (<i>Larus atricilla</i>)	23.0	—	—	—
Black-legged Kittiwake (<i>Rissa tridactyla</i>)	33.2	37.4	48.1	15.0
Heermann's Gull (<i>Larus heermanni</i>)	27.8	36.8	46.6	18.4 ^d
Common Puffin (<i>Fraterecula arctica</i>)	33.8	—	—	—
Royal Tern (<i>Sterna maxima</i>)	24.0	37.8	49.2	25.2
Lesser Black-backed Gull (<i>Larus fuscus</i>)	23.7	—	—	—
Herring Gull (<i>Larus argentatus</i>)	27.4	38.3	50.5	23.0
Glaucous-winged Gull (<i>Larus glaucescens</i>)	24.6	36.0	44.6	20.0
Western Gull (<i>Larus occidentalis livens</i>)	35.6	33.8 ^c	39.5	26.1 ^d
South Polar Skua (<i>Catharacta maccormicki</i>)	35.5	36.0	44.6	9.0
Great Black-backed Gull (<i>Larus marinus</i>)	29.9	—	—	—
	<u>28.0</u>	<u>36.4</u>	<u>45.6</u>	<u>19.6</u>
Pelecaniformes				
Tropical				
Red-footed Booby (<i>Sula sula</i>)	28.8	36.0	44.6	15.8
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	22.2	36.0	44.6	22.4
Great Frigatebird (<i>Fregata minor</i>)	25.9	36.8	46.6	20.7
	<u>25.6</u>	<u>36.3</u>	<u>45.3</u>	<u>19.6</u>

^a Boersma et al. 1980.

^b Howell and Bartholomew 1962.

^c Bennett et al. 1981.

^d Measured directly by egg hygrometry (Rahn et al. 1977).

^e Grant 1982.

TABLE 6
 FRESH-EGG MASS (W), NEST VENTILATION (V_{nest}), WATER-VAPOR PRESSURE IN THE NEST ($P_{\text{H}_2\text{O, nest}}$) AND AMBIENT
 WATER-VAPOR PRESSURE ($P_{\text{H}_2\text{O, air}}$) FOR SEVEN SPECIES OF SEABIRDS

Order Species	W (g)	V_{nest} (l/day)	$P_{\text{H}_2\text{O, nest}}$ (torr)	$P_{\text{H}_2\text{O, air}}$ (torr)	$P_{\text{H}_2\text{O, nest}}$	Reference
					$- P_{\text{H}_2\text{O, air}}$ (torr)	
Procellariiformes						
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	39.5	36.5	18.1	14.9	3.2	Grant et al. 1982a
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	60.0	70.9	19.6	17.3	2.3	Whittow et al. 1982
Laysan Albatross (<i>Diomedea immutabilis</i>)	285.0	133.0	19.1	13.7	5.4	Grant et al. 1982b
Black-footed Albatross (<i>Diomedea nigripes</i>)	305.0	209.0	17.3	13.7	3.6	Grant et al. 1982b
Charadriiformes						
Black-legged Kittiwake (<i>Rissa tridactyla</i>) ^a	51.5	39.7	15.0	6.4	8.6	Morgan et al. 1978
Heermann's Gull (<i>Larus heermanni</i>) ^a	53.4	81.0	18.4	14.4	4.0	Rahn and Dawson, 1979
Glaucous-winged Gull (<i>Larus glaucescens</i>) ^a	98.2	44.0	20.0	6.4	13.6	Morgan et al. 1978

^a Breeding outside the tropics.

loss from the egg = water lost from the nest; C_{nest} and C_{air} = water-vapor content of air in the nest microclimate and ambient air, respectively. Water loss from the egg may be measured directly and so may water-vapor content of ambient air, if air temperature and either air relative humidity or its water-vapor pressure are measured. The value for C_{nest} may be calculated if the mean temperature of the nest microclimate is taken to be 34°C (Drent 1975) and the nest microclimate water-vapor pressure has been measured by egg hygrometry or calculated as described above.

Morgan et al. (1978) calculated nest ventilation for two Alaskan gulls sharing the same ambient conditions (Table 6). The egg of the Glaucous-winged Gull (*Larus glaucescens*) was almost twice as large as that of the Black-legged Kittiwake (*Rissa tridactyla*). Other things being equal, one might expect the larger egg, with its greater water loss, to require a considerably greater ventilation of its nest. However, nest ventilation of the gull was only 10.8% greater. This might be attributed to higher nest water-vapor pressure (20 torr) for the gull than for kittiwake (15 torr), with a correspondingly greater difference in water-vapor pressure between nest and ambient air. Thus, the kittiwake's nest might require relatively more ventilation because of a smaller difference in $P_{\text{H}_2\text{O, nest}} - P_{\text{H}_2\text{O, air}}$. These data invite comparison with calculated nest ventilation for Heermann's Gulls (*Larus heermanni*) breeding under warm conditions off the Mexican coast (Rahn and Dawson 1979). The size of the egg is similar in the Black-legged Kittiwake and Heermann's Gull. However, ambient water-vapor pressure is higher in Heermann's Gulls with a

correspondingly lower difference in ($P_{\text{H}_2\text{O, nest}} - P_{\text{H}_2\text{O, air}}$) and a greater requirement for nest ventilation (Table 6). Considerations of nest ventilation in the gulls is complicated by differences in clutch size. Bonin Petrels, *Pterodroma hypoleuca* and Wedge-tailed Shearwaters are two Procellariiforms that lay a single egg in a burrow in the ground. Of the seven species included in Table 6, these two species have lowest values for $P_{\text{H}_2\text{O, nest}} - P_{\text{H}_2\text{O, air}}$. Nest ventilation of Bonin Petrels is not much less than that for the larger egg of Black-legged Kittiwakes. Nest ventilation for Wedge-tailed Shearwaters is well above that for the larger egg of Glaucous-winged Gulls, *Larus glaucescens*. In two species of albatross investigated by Grant et al. (1982b), a single egg is laid, and the eggs are similar size. Nevertheless, nest ventilation required by Black-footed Albatross was 57% greater than that for Laysan Albatross, reflecting the lower water-vapor pressure in the Black-footed Albatross' nest and the smaller difference in water-vapor pressure between its nest and surroundings. However, direct observations of birds revealed a greater frequency of nest ventilating behavior by Laysan Albatrosses! In fact, Walsberg (1980) calculated that, in general, changes in nest ventilation would be relatively ineffective in regulating water loss from the egg. He subsequently produced evidence that two species of terrestrial birds did not actively regulate nest humidity (Walsberg 1983).

Calculation of nest ventilation is subject to three errors. In the first place, the computation does not include water loss from the incubation patch. Therefore total water loss must exceed water loss from the egg by an unknown amount. Nevertheless, nest ventilation as computed does

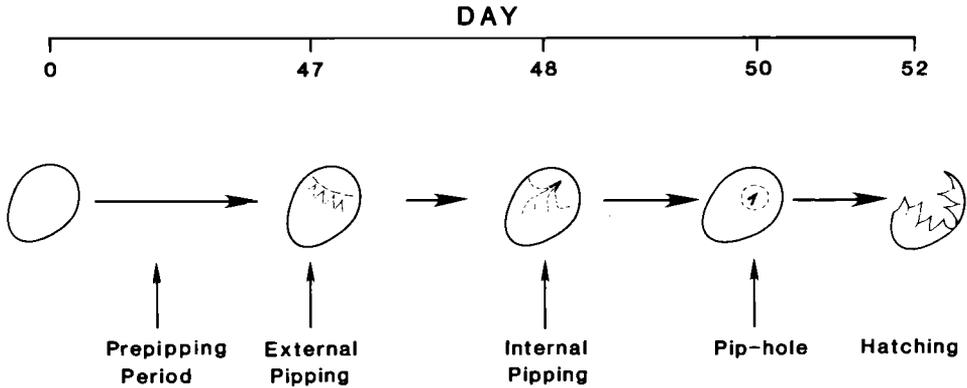


FIGURE 12. Sequence of events during pipping in Wedge-tailed Shearwaters (Pettit and Whittow 1982b).

represent the minimal ventilation necessary to dissipate water lost from the egg itself. Another error arises from the assumption that nest temperature is 34°C. Nest temperature has never been measured satisfactorily; it is a heterogeneous temperature and its exact measurement would require measurement of area and temperature of the interface between egg and feathers, and egg and nest material. Nest temperatures should then be a weighted mean of these measurements. The concept of nest ventilation is potentially useful, because it assigns quantitative values to behavioral phenomena. I hope that future applications of the equation for nest ventilation will employ measurements of water loss from the skin of the incubating bird together with measured values of nest temperature. A third error arises from the use of daily rate of water loss from unpipped eggs. While this would be appropriate before the egg is pipped, it would underestimate nest ventilation from pipped eggs, from which water loss is very much greater (see following section).

WATER LOSS FROM PIPPED EGGS

In many species of tropical seabirds, the initial event in the pipping process is a series of star fractures in the shell. This may occur up to a week before emergence of the hatchling. The implications of star fracturing of the shell, for water loss from the egg, are considerable. Prior to star fracturing, which has been referred to as "external pipping" by the present author and his colleagues, water loss from the egg can occur only by diffusion through pores in the shell. Shell fracture, however, effectively establishes a leak through the shell, and then water loss through the shell is, not surprisingly, higher.

In shearwaters and petrels, and also in the terns that have been studied, the next event in the pipping process is penetration of the air cell by

the beak of the embryo (Fig. 12). This event ("internal pipping") has little effect on water loss from the egg, although it marks the beginning of embryonic pulmonary ventilation, the embryo rebreathing gas in the air cell. However, establishment of a distinct hole ("pip-hole"—some investigators have termed this phenomenon "external pipping") in the shell, provides further opportunities for increased water loss, including from the respiratory tract of the embryo. The duration of the pipping phase (from star fracture to hatching) is short in relation to total duration of incubation. However, the augmented water loss during this period means that total water loss from the pipped egg is a significant fraction of cumulative water loss from the egg during the entire incubation period (Table 7). In the six species included in Table 7, water loss between star fracture and hatching was as high as 42% of cumulative water loss over the entire incubation period. In the two species of albatross the water loss from pipped eggs amounted to only 9–11% of total water loss from the egg. The pipping sequence in albatross differs from that in petrels, shearwaters and terns. In the albatross, internal pipping is the initial event, followed by star fracture. The interval between star fracture and hatching is correspondingly shorter in the albatross (Table 7). Therefore, in four Procellariiformes and two Charadriiformes, total water loss from star fractured eggs, expressed as a percentage of cumulative water loss from the egg, parallels the duration of the interval between star fracture and hatching. It is noteworthy that, in this small series of tropical procellariiform seabirds, in which egg size varied by a factor of more than seven, there was a change in sequence of pipping with increasing egg size, and also a definite change in both relative duration of the interval between star fracture and hatching, and

the fraction of total water loss that is lost during this interval. It may also be pertinent that the incubation period of smaller eggs is relatively longer than those of the larger albatross eggs (see Discussion). Thus, there may be a correlation between sequence of pipping, size of the egg, duration of its pipping phase, and fractional water loss from piped eggs. A corollary to these observations is that total water loss during the pre-pipping period is relatively large in bigger eggs (Table 7).

TOTAL WATER LOSS FROM THE EGG

In contrast to the different way in which water loss is partitioned between the pre-pipping period and the pip-to-hatch interval (Table 7), cumulative water loss over the entire incubation period, expressed as a fraction of the fresh-egg mass, did not vary greatly in six species (Table 7). These observations, although limited in scope, are compatible with the belief that total water loss from the egg is a closely regulated fraction of fresh-egg mass. This belief conforms also with evidence presented by Ar and Rahn (1980) that water content of the freshly laid egg and of the hatchling, are very similar. Thus, in six charadriiform seabirds, mean water content of freshly laid egg and hatchling was 77.2 and 78.2%, respectively.

OXYGEN UPTAKE BY THE EGG

DAILY RATE OF EMBRYONIC OXYGEN CONSUMPTION (\dot{V}_{O_2} , \dot{M}_{O_2})

The rate of oxygen transfer into the egg through the shell is equal to the rate of oxygen consumption by the embryo. Unlike the rate of water loss from the egg, which is constant over a large part of the incubation period, oxygen uptake by the egg increases as the embryo grows (e.g., Ackerman et al. 1980). The pattern of increase in oxygen consumption with time, for two tropical Procellariiformes, is illustrated in Figure 13. A similar pattern has been reported for Leach's Storm-Petrel (Rahn and Huntington, pers. comm.) and the Fork-tailed Storm-Petrel (Vleck and Kenagy 1980), two species from higher latitudes. As the mode of development of all four species is similar, a similar pattern of increase in oxygen consumption is expected (Vleck et al. 1980), but does not necessarily follow. Pettit et al. (1981, 1982a, b) considered a logistic equation to best describe the data.

Rahn and Ar (1974), Hoyt et al. (1978) and Hoyt and Rahn (1980) established a relationship between oxygen uptake immediately prior to internal pipping, and fresh-egg mass. In those eggs in which internal pipping is the initial event in the pipping process, this is a valid point of ref-

TABLE 7
TIME INTERVAL AND WATER LOSS BETWEEN (A) THE LAYING OF THE EGG AND STAR FRACTURE OF THE SHELL (PRE-PIPPING), (B) STAR-FRACTURE OF THE SHELL AND HATCHING (PIP-HATCH) AND THE TOTAL WATER LOSS FROM THE EGG IN SIX SPECIES OF TROPICAL SEABIRDS

Order Species	W^a (g)	P^b (days)	Total water loss (g)	Total water loss (% of W)	Pre-pipping period (% of I)	Pre-pipping water loss (% of total water loss)	Pip-hatch interval (% of I)	Pip-hatch water loss (% of total)	Reference
Procellariiformes									
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	39.2	48.7	7.3	18.6	87.7	65.1	12.1	34.9	Grant et al. 1982a
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	60.0	52.0	10.7	17.2	90.8	71.0	9.2	29.0	Whittow et al. 1982, Pettit and Whittow 1982b
Laysan Albatross (<i>Diomedea immutabilis</i>)	284.8	65.0	45.7	16.0	95.1	91.2	4.9	8.8	Grant et al. 1982b
Black-footed Albatross (<i>Diomedea nigripes</i>)	304.9	66.0	49.2	16.1	94.4	88.9	5.6	11.1	Grant et al. 1982b
Charadriiformes									
White Tern (<i>Gygis alba</i>)	23.3	35.5	4.1	17.6	85.4	58.0	14.6	42.2	Pettit et al. 1981
Gray-backed Tern (<i>Sterna lunata</i>)	28.7	30.3	4.1	14.3	86.5	68.3	13.5	31.7	Whittow, Grant, Flint and Pettit, unpubl. data

^a Fresh-egg mass.

^b Incubation period.

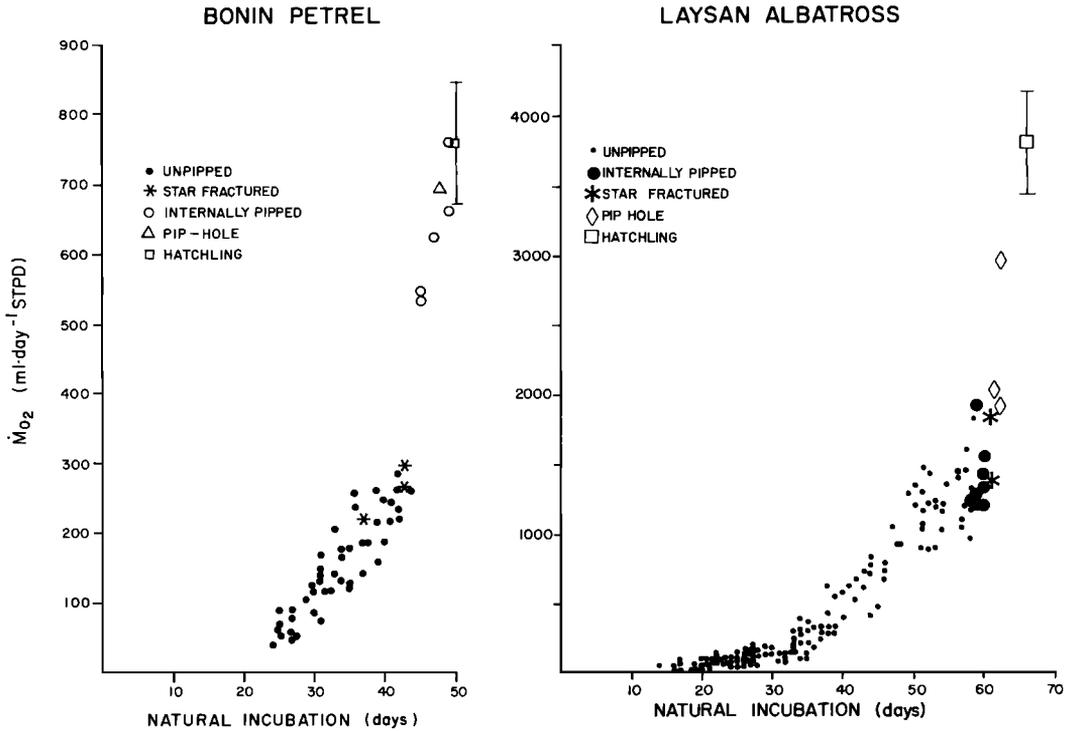


FIGURE 13. Embryonic oxygen consumption (\dot{M}_{O_2}) during natural incubation in Bonin Petrel, *Pterodroma hypoleuca*, and Laysan Albatross, *Diomedea immutabilis*, After Pettit et al. (1982a, b).

erence for comparisons between species. Prior to internal pipping oxygen can diffuse into the egg only through pores in the eggshell and it does so under influence of a difference in partial pressure of oxygen between gas inside the egg (air cell) and that in the microclimate of the egg (see below). Once internal pipping has occurred, partial pressure of oxygen in the air cell diminishes because the embryo rebreathes gas in the air cell. The increased difference in oxygen partial pressure (ΔP_{O_2}) results in an increased rate of diffusion of oxygen into the egg. The extent of this increase depends on the degree to which the embryo rebreathes the air in the air cell. In eggs in which star fracture is the initial pipping event, an increase in oxygen uptake occurs because fractures in the shell establish a "leak." The magnitude of the increase depends on the degree to which the shell is fractured (Pettit et al. 1982a). Since this happens before internal pipping occurs, oxygen uptake subsequent to star fracture, but prior to internal pipping, is likely to be variable. Consequently, the pre-internal pipping point in time is not a good reference point for comparative purposes. In such eggs, oxygen uptake immediately prior to star fracture is a valid time

for reference purposes. At that time, the shell has not been fractured and the air cell has not been penetrated. If comparisons are to be made between species in which the pipping sequence differs, then the reference point should be immediately before the initial event in the pipping process, be it star fracture or internal pipping (Pettit and Whittow 1982a). Pettit and Whittow (1982a) showed that air-cell partial pressures of oxygen and carbon dioxide are very similar prior to the initial event in the pipping process, irrespective of whether this event is star fracture or internal pipping. Both star-fracture and internal pipping result in an increase in oxygen consumption by the embryo. Therefore, the time of incubation immediately prior to the initial event in the pipping process, regardless of whether this is star-fracture or internal pipping, represents a period in which air-cell gas tensions appear to be similar in all or most eggs, and the integrity of the shell and shell membranes has not been violated. Oxygen uptake of the egg at this point is determined by pore geometry of the eggshell and the difference in oxygen partial pressure between the air cell and the air surrounding the egg. As the latter difference is similar in all eggs, oxy-

TABLE 8
 OXYGEN CONSUMPTION (\dot{V}_{O_2}) OF THE EMBRYO IMMEDIATELY PRIOR TO THE INITIAL EVENT IN THE PIPPING PROCESS, TOGETHER WITH THE OXYGEN CONSUMPTION OF THE NEWLY-HATCHED CHICK, IN SEVEN SPECIES OF TROPICAL SEABIRDS

Order Species	W^a (g)	Embry- onic pre- pipping \dot{V}_{O_2} (ml·O ₂ / day)	Hatch- ling \dot{V}_{O_2} (ml·O ₂ / day)	Embry- onic pre- pipping \dot{V}_{O_2} (% of hatch- ling \dot{V}_{O_2})	Reference
Procellariiformes					
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	39.2	246	757	32.5	Pettit et al. 1982b
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	60.0	304	840	36.2	Ackerman et al. 1980
Laysan Albatross (<i>Diomedea immutabilis</i>)	284.8	1250	3820	32.7	Pettit et al. 1982a
Black-footed Albatross (<i>Diomedea nigripes</i>)	304.9	1225	3680	33.3	Pettit et al. 1982a
Charadriiformes					
White Tern (<i>Gygis alba</i>)	23.3	159	470	33.8	Pettit et al. 1981
Black Noddy (<i>Anous tenuirostris</i>)	24.8	184	524	35.1	Pettit and Whittow, unpubl. data
Brown Noddy (<i>Anous stolidus</i>)	40.1	283	690	41.0	Pettit and Whittow, unpubl. data

^a W = Fresh-egg mass.

gen uptake is determined largely by pore geometry of the shell and intrinsic metabolic machinery of the embryo. At this stage the functional pore area of the shell is potentially a limiting factor in oxygen uptake. In Table 8 oxygen uptake of eggs of seven tropical seabirds, just prior to the initial pipping event, is expressed as a percentage of oxygen consumption of the newly-hatched chick, which represents the end product of incubation. The pre-pipping rate of oxygen consumption varied from 32.5 to 41.0% of hatchling rate. Within the Procellariiformes included in Table 8, there was little evidence of any trend, but in the three tropical Charadriiformes, the pre-pipping embryonic oxygen consumption was relatively lowest in the White Tern and highest in the Brown Noddy. The White Tern has the longest incubation period relative to its egg mass. The significance of this is indicated in the discussion.

It is difficult to compare the tropical species in Table 8 with species from higher latitudes, because of uncertainty regarding pipping sequence in the latter species, and because embryonic oxygen consumption was measured after star fracture had occurred. Thus, in data presented by Vleck and Kenagy (1980) for the Fork-tailed Storm-Petrel, "pre-pipping" oxygen consumption was 61.4% of that of the hatchling. The eggs were reported to have hatched "within 1 or 2 days of pipping" but it is uncertain whether "pipping" refers to star fracture, internal pipping or formation of a pip hole. If oxygen consump-

tion was measured three days prior to hatching, the value would be expected to be high, by comparison with other Procellariiformes, because star fracture would have already occurred. With regard to "the chicken," it is possible to be more exact: pre-internal pipping embryonic oxygen consumption represented 49.0% of that of the hatchling (Freeman and Vince 1974). In "the chicken," internal pipping is the initial event in the pipping process. Hoyt and Rahn's (1980) relationship between pre-internal pipping oxygen consumption and fresh-egg mass was derived from 27 species of birds. Unfortunately, in some species, internal pipping was not the initial pipping event so oxygen consumption of these species was presumably elevated as a result of star fracture. This would have the effect of elevating oxygen consumption predicted on the basis of fresh-egg mass. With this reservation in mind, the values shown in Table 8 were all lower than predictions based on fresh-egg mass (W), using Hoyt and Rahn's (1980) equation:

$$\dot{V}_{O_2} = 28.9 W^{0.714} \quad (\text{ml/day}) \quad (\text{g})$$

The measured values ranged from 56.5% of predictions for the Wedge-tailed Shearwater to 76.5% for the Laysan Albatross. However, in the Common Tern (Rahn et al. 1974) and the Royal Tern (Vleck, Vleck, Rahn and Paganelli, pers. comm.), two terns nesting outside the tropics, pre-internal pipping \dot{V}_{O_2} was also lower than predictions. In

TABLE 9

OXYGEN CONDUCTANCE OF THE SHELL (G_{O_2}), PARTIAL PRESSURE OF OXYGEN IN THE AIR CELL ($P_{O_2,egg}$) AND IN THE AIR SURROUNDING THE NEST ($P_{O_2,air}$), TOGETHER WITH THE DIFFERENCE BETWEEN $P_{O_2,egg}$ AND $P_{O_2,air}$ (ΔP_{O_2}), IN SEVEN SPECIES OF TROPICAL SEABIRDS

Order Species	G_{O_2} (measured) ^a (ml/day torr)	G_{O_2} (calculated) ^b (ml/day torr)	$P_{O_2,egg}$ (torr)	$P_{O_2,air}$ (torr)	ΔP_{O_2} (torr)	Reference
Procellariiformes						
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	4.9	5.6	100.6	150.5	49.9	Pettit et al. 1982b
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	7.6	6.6	100.8	149.3	48.5	Ackerman et al. 1980
Laysan Albatross (<i>Diomedea immutabilis</i>)	30.5	34.7	106.0	156.3	50.3	Pettit et al. 1982a
Black-footed Albatross (<i>Diomedea nigripes</i>)	29.5	34.2	106.0	156.3	50.3	Pettit et al. 1982a
Charadriiformes						
White Tern (<i>Gygis alba</i>)	3.0	2.7	100.3	153.6	53.3	Pettit et al. 1981
Black Noddy (<i>Anous tenuirostris</i>)	3.7	4.9	98.5	153.6	54.1	Pettit and Whittow, unpubl. data
Brown Noddy (<i>Anous stolidus</i>)	4.4	7.5	92.1	153.6	61.5	Pettit and Whittow, unpubl. data

^a Rahn et al (1974); $G_{O_2} = \dot{V}_{O_2} / \Delta P_{O_2}$
^b Hoyt et al. (1979); $G_{O_2, 38^\circ C} = 1.08 G_{H_2O, 25^\circ C}$

the Herring Gull (another non-tropical species), on the other hand, oxygen consumption immediately prior to internal pipping was 116% of the expected value based on fresh-egg mass (Rahn et al. 1974). It is difficult to draw conclusions from these figures particularly in view of the uncertainty regarding the precise point in the pipping sequence that measurements of \dot{V}_{O_2} were made.

This discussion should not end without drawing attention to the fact that immediately prior to the initial event in the pipping process, the embryonic mass will not necessarily be the same even in eggs of similar fresh-egg mass. In future work, it would seem important to measure oxygen consumption immediately prior to the initial pipping event and to relate oxygen consumption to yolk-free mass of the embryo. Once such a relationship between yolk-free embryonic mass and oxygen consumption has been established, comparisons will be possible between different species with different shell gas conductances, incubation times and other factors.

OXYGEN CONDUCTANCE OF THE SHELL (G_{O_2})

As far as can be ascertained from the preceding analysis, the rate of embryonic oxygen consumption immediately before the initial pipping event is relatively low in tropical seabirds. Oxygen consumption is determined by oxygen conductance of the shell and shell membranes on one hand, and the difference in partial pressure of oxygen across the shell (ΔP_{O_2}) on the other:

$$\dot{V}_{O_2} = G_{O_2} \cdot \Delta P_{O_2}$$

(ml/day) (ml/day · torr) (torr)
(Rahn et al. 1974)

The low value for water-vapor conductance of the shell of many tropical seabirds, as described previously, implies that oxygen conductance of the shell is also low, because water vapor and oxygen diffuse through the same pores. Conductance to water vapor and oxygen is in fact proportional to their respective diffusion coefficients (Paganelli et al. 1978). Consequently, if the value for G_{H_2O} is known, the G_{O_2} may be calculated:

$$G_{O_2, 38^\circ C} = 1.08 G_{H_2O, 25^\circ C}$$

(ml/day · torr) (mg/day torr)
(Hoyt et al. 1979)

If the \dot{V}_{O_2} is measured, together with the partial pressure of oxygen in the air cell and air surrounding the egg, a value for G_{O_2} may be calculated. In Table 9 values for G_{O_2} computed from the G_{H_2O} , and from the \dot{V}_{O_2} and ΔP_{O_2} , are presented for a small number of tropical species. There is some disparity in the data but, in general, they lead to the conclusion that oxygen conductance, like water-vapor conductance, is relatively low in the tropical species that have been studied.

OXYGEN PARTIAL PRESSURE DIFFERENCE (ΔP_{O_2})

Attention was drawn in a preceding section to the fact that the oxygen partial pressure in the

TABLE 10
PARTITION OF THE TOTAL AMOUNT OF OXYGEN CONSUMED DURING INCUBATION BETWEEN THE PRE-PIPPING PERIOD AND THE PERIOD FROM THE INITIATION OF PIPPING TO HATCHING, IN 12 SPECIES OF SEABIRDS

Order Species	Total oxygen consumption		Pre-pipping ^a oxygen consumption		Pip ^a -to-hatch oxygen consumption		Reference
	ml	ml/g-fresh-egg mass	ml	% of total	ml	% of total	
Procellariiformes ^b							
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>) ^c	1870	179.0	—	—	—	—	Rahn and Huntington, pers. comm.
Fork-tailed Storm-Petrel (<i>Oceanodroma furcata</i>) ^c	2830	207.9	—	—	—	—	Vleck and Kenagy 1980
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	5610	143.1	2790	50.0	2820	50.0	Pettit et al. 1982b
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	7776	132.5	4574	57.6	3202	42.4	Ackerman et al. 1980; Pettit et al. 1982b
Laysan Albatross (<i>Diomedea immutabilis</i>)	29,671	104.2	17,271	58.2	12,400	41.8	Pettit et al. 1982a
Black-footed Albatross (<i>Diomedea nigripes</i>)	30,246	99.2	17,500	58.1	12,746	41.9	Pettit et al. 1982a
Charadriiformes ^b							
Common Tern (<i>Sterna hirundo</i>) ^c	1599	78.0	—	—	—	—	Rahn et al. 1974
White Tern (<i>Gygis alba</i>)	2565	110.0	1490	58.1	1075	41.9	Pettit et al. 1981
Black Noddy (<i>Anous tenuirostris</i>)	3180	128.2	1532	48.2	1648	51.8	Pettit and Whittow, unpubl. data
Brown Noddy (<i>Anous stolidus</i>)	4780	119.2	2400	50.2	2380	49.8	Pettit and Whittow, unpubl. data
Royal Tern (<i>Sterna maxima</i>) ^c	5236	77.0	—	—	—	—	Vleck et al. 1980
Herring Gull (<i>Larus argentatus</i>) ^c	9669	110.0	—	—	—	—	Rahn et al. 1974

^a "Pip" and "pipping" refers to the initial event in the pipping process.

^b In both Procellariiformes and Charadriiformes the species are arranged in order of increasing egg mass.

^c Breeding outside the tropics.

air-cell gas, immediately prior to initiation of pipping is very similar in different species (Table 9). In two species of seabirds from higher latitudes, Common Tern (*Sterna hirundo*) and Herring Gull (*Larus argentatus*), oxygen partial pressure in the air cell was 108.7 and 99.7 torr, respectively (Rahn et al. 1974), close to values reported for tropical seabirds (Table 9). There is some uncertainty as to whether the shells of the tern and gull had star fractured, which is known to increase the P_{O_2} in the air cell (Pettit and Whittow 1982). The partial pressure of oxygen in the air surrounding the nest was rather lower in burrowing species (petrel and shearwater), as might be expected. However, the difference in oxygen pressure across the eggshell was similar in all seven species (Table 9) except for the Brown Noddy, a surface nesting species. The greater ΔP_{O_2} for the Brown Noddy was due to a relatively low $P_{O_2,egg}$ (Table 9).

TOTAL OXYGEN CONSUMED DURING INCUBATION

The total amount of oxygen consumed by the embryo, over the entire incubation period, for

several species, is presented in Table 10. Hoyt and Rahn (1980) claimed that the total amount of oxygen consumed during incubation averaged 102 ml/g fresh-egg mass. This figure was based on data from 27 species, individual species ranged from 61 to 141 ml/g. It is clear from Table 10 that several procellariiform seabirds, particularly the smaller petrels, lie outside this range and well above the mean value of 102 ml/g. It is also apparent from Table 10 that the two petrels from higher latitudes (Fork-tailed Storm-Petrel and Leach's Storm-Petrel) had the highest total oxygen cost of incubation. However, these two species also had the smallest eggs listed in Table 10. Consequently, the greater oxygen cost of incubation in these two species may reflect size of their eggs rather than the geographical situation of their breeding colony. Among Charadriiformes, the Black Noddy had the highest total oxygen consumption; there was little evidence of a relationship between the total amount of oxygen consumed and the fresh-egg mass in this order.

Although the period between first indication

TABLE 11
CARBON DIOXIDE PARTIAL PRESSURE IN THE AIR CELL OF THE EGG ($P_{\text{CO}_2, \text{egg}}$) AND IN THE AIR SURROUNDING THE NEST ($P_{\text{CO}_2, \text{air}}$) FOR PROCELLARIIFORM AND CHARADRIIFORM SEABIRDS

Order Species	$P_{\text{CO}_2, \text{egg}}$ (torr)	$P_{\text{CO}_2, \text{air}}$ (torr)	$\frac{\Delta P_{\text{CO}_2}}{P_{\text{CO}_2, \text{air}}}$ (torr)	Reference
Procellariiformes				
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	45.5	5.0	40.5	Pettit et al. 1982b
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	41.8	0.5	41.3	Ackerman et al. 1980
Laysan Albatross (<i>Diomedea immutabilis</i>)	40.0	0.3	39.7	Pettit et al. 1982a
Black-footed Albatross (<i>Diomedea nigripes</i>)	40.0	0.3	39.7	Pettit et al. 1982a
Charadriiformes				
Common Tern (<i>Sterna hirundo</i>) ^a	32.8	0.3	32.5	Rahn et al. 1974
White Tern (<i>Gygis alba</i>)	48.5	0.3	48.2	Pettit et al. 1981
Black Noddy (<i>Anous tenuirostris</i>)	42.3	0.3	42.0	Pettit and Whittow, unpubl. data
Brown Noddy (<i>Anous stolidus</i>)	46.6	0.3	46.3	Pettit and Whittow, unpubl. data
Herring Gull (<i>Larus argentatus</i>) ^a	36.2	0.3	35.9	Rahn et al. 1974

^a Breeding outside the tropics.

of pipping and hatching of the chick is short in relation to total length of incubation, it is clear that a substantial fraction of total oxygen consumption of the embryo occurs during this interval. In the Bonin Petrel and Black Noddy more than half of total oxygen consumption took place in the last 12.1% and 15.0%, respectively, of the total incubation period. Unfortunately, it is not possible to compare tropical species with seabirds from higher latitudes, in this regard, because no data for the latter exist.

CARBON DIOXIDE PRODUCTION BY THE EMBRYO

Few measurements of carbon dioxide production by the embryo have been made in seabirds. Partial pressure of carbon dioxide in the air-cell gas immediately prior to initiation of pipping has, however, been recorded in a number of species (Table 11). Values are rather lower for the two species breeding outside the tropics (Common Tern and Herring Gull) but as there is uncertainty regarding the exact point during the pipping process that air-cell gas was sampled in these two species, it is premature to draw any conclusions. Partial pressure of carbon dioxide in deep burrows of Bonin Petrels was 5.0 torr (Pettit et al. 1982b), considerably above that of fresh air. The P_{CO_2} in air-cell gas in this species was 45.5 torr, resulting in a value for ΔP_{CO_2} of 40.5, very similar to that for other seabirds and for birds in general (Rahn et al. 1974).

HEAT TRANSFER BETWEEN PARENT BIRD AND THE EGG

Direct measurements of heat transfer between parent bird and the egg have not been made in any seabird. Incubation patch temperatures have

been measured in some species, and, in conjunction with central egg temperatures, provide a measure of the difference in temperature responsible for heat flow from bird to egg (Table 12). The smallest difference between incubation patch temperature and egg temperature was recorded in the Bonin Petrel, a tropical, burrow-nesting species. The greatest difference was for another petrel, Fork-tailed Storm-Petrel, which breeds in cold conditions. However, the magnitude of the difference ($T_{ip} - T_{\text{egg}}$) for the latter species partly reflects the very low egg temperature. Data presented in Table 12 must be considered in the perspective that both incubation patch and egg temperatures have been measured by a variety of procedures, and at different stages of incubation.

Although heat transfer to the egg has not been measured directly, it may be estimated from attempts to determine the energy cost to the parent of incubating the egg. Such attempts have been made for petrels and penguins by Croxall (1982). Estimates were based on weight loss of incubating birds: daily energy expenditure was 1.3–1.4 times basal metabolic rates. Thus, an albatross or shearwater, with basal metabolic rates of 443 kcal/day or 22 kcal/day, respectively, would expend an additional 70 or 13 kcal/day in order to incubate the single egg. Direct measurements of oxygen consumption of incubating Laysan Albatross and Bonin Petrels led Grant and Whittow (1983) to conclude that metabolic rates of incubating birds were below or equal to basal metabolic rates, separately measured. These results imply that the Laysan Albatross and Bonin Petrel did not need to generate additional heat in order to incubate their egg. It implies also, and this is an important point, that the thermal conduc-

TABLE 12
INCUBATION PATCH (T_{ip}) AND CENTRAL EGG (T_{egg}) TEMPERATURES IN SEABIRDS

Order Species	T_{ip} (°C)	T_{egg}^b (°C)	$T_{ip} - T_{egg}$ (°C)	Reference
Procellariiformes				
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>) ^a	35.8	33.4	2.4	Rahn and Huntington, pers. comm.
Fork-tailed Storm-Petrel (<i>Oceanodroma furcata</i>) ^a	37.6	29.7	7.9	Wheelwright and Boersma 1979
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	34.9	33.8	1.1	Grant, Pettit, Whittow, Rahn and Paganelli, unpubl. data
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	37.6	35.0	2.6	Whittow et al. 1982
Laysan Albatross (<i>Diomedea immutabilis</i>)	38.7	35.8	2.9	Grant, Pettit, Whittow, Rahn and Paganelli, unpubl. data
Black-footed Albatross (<i>Diomedea nigripes</i>)	38.3	35.0	3.3	Grant, Pettit, Whittow, Rahn and Paganelli, unpubl. data
Charadriiformes				
White Tern (<i>Gygis alba</i>)	36.7	35.3	1.4	Pettit et al. 1981
Sooty Tern (<i>Sterna fuscata</i>)	39.6	35.7	3.9	Howell and Bartholomew 1962
Black-legged Kittiwake (<i>Rissa tridactyla</i>) ^a	38.9	37.4	1.5	Barrett 1980
Herring Gull (<i>Larus argentatus</i>) ^a	40.5	38.3	2.2	Drent 1970
Great Skua (<i>Catharacta skua</i>) ^a	39.3	35.6	3.7	Drent 1970
South Polar Skua (<i>Catharacta maccormicki</i>) ^a	39.0	36.0	3.0	Spellerberger 1969

^a Breeding outside the tropics.

^b Taken from Table 5.

tance of the egg is similar to that of the feathers dropped when birds develop their incubation patch.

DISCUSSION

The foregoing analysis has brought to light a number of apparent differences between tropical seabirds and their counterparts in higher latitudes. In a previous review of incubation in seabirds (Whittow 1980) it was recognized that prolonged incubation was a common feature of tropical seabirds. In Figure 14, the line represents the relationship between incubation period (I) and fresh-egg mass (W), for birds in general:

$$I = 12.03 W^{0.217} \quad (\text{Rahn and Ar 1974})$$

(days) (g)

As far as Procellariiformes are concerned, all species included in Fig. 14 had longer incubation periods than the expected values based on egg mass. The limited data suggest there was no difference between tropical and non-tropical species in this respect. The tropical Charadriiformes also had long incubation periods and so also did three alcids breeding outside the tropics. However, incubation periods of most Charadriiformes from

higher latitudes were close to or below predicted values (Fig. 14). The limited information on Pelicaniformes indicates that all tropical species have relatively long incubation periods. These conclusions conform with those made previously (Whittow 1980).

To what extent can the differences between tropical and non-tropical sea birds be attributed to longer incubation times of the former? An attempt can be made to answer this question for daily rate of water loss from the egg. Thus, Ar and Rahn (1980) have shown that for birds in general, daily rate of water loss (\dot{M}_{H_2O}) may be related to the fresh-egg mass (W) and to incubation period (I) in the following way:

$$\dot{M}_{H_2O} = 130.4 \frac{W^{0.977}}{I^{0.937}} \quad (\text{Ar and Rahn 1980})$$

(mg/day) (g/day)

This equation essentially provides a predicted value for \dot{M}_{H_2O} , based on fresh-egg mass and incubation time. In Table 13 daily rates of water loss, expressed in this way, are presented for tropical members of the three orders of seabirds. In tropical Procellariiformes, measured daily rate of water loss was considerably lower than the value predicted solely on the basis of fresh-egg

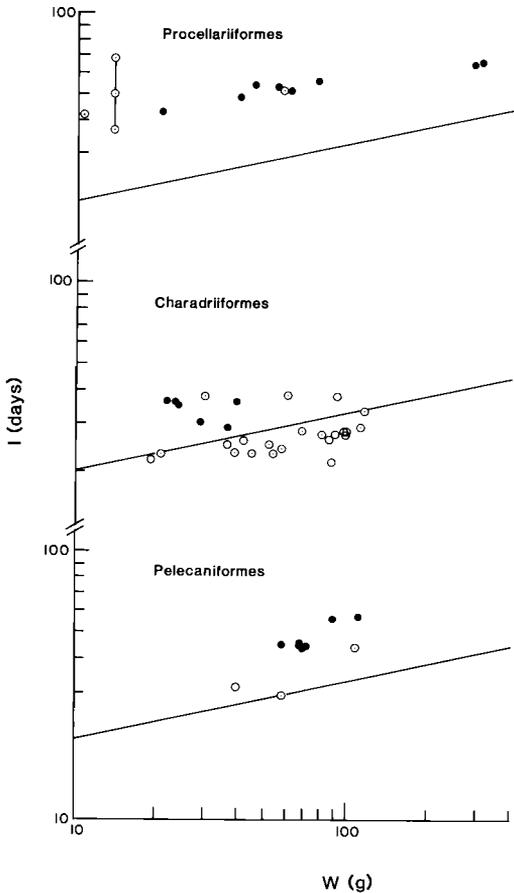


FIGURE 14. Relationship between incubation period (*I*) and fresh-egg mass (*W*) in seabirds for which data on other aspects of their incubation physiology are available. ● = tropical species; ○ = species from higher latitudes. The three points connected by a vertical line are incubation periods for Fork-tailed Storm-Petrels, which vary with degree of egg neglect (Boersma and Wheelwright 1979). The line represents the relationship $I = 12.03 W^{0.217}$ (Rahn and Ar, 1974). Data from Rice and Kenyon 1962, Fordham 1964a, b, Harris, 1966, Ashmole and Ashmole 1967, Lack, 1968, Kepler 1969, Nelson 1969, 1971, Fisher 1971, Shallenberger 1973, Fleet 1974, Rahn et al. 1976, Ar and Rahn 1978, Morgan et al. 1978, Rahn and Dawson 1979, Ricklefs and Montevecchi 1979, Hoyt and Rahn, 1980, Roudybush et al. 1980, Vleck and Kenagy 1980, Pettit et al. 1981, Pettit et al. 1982a, Rahn and Huntington, pers. comm., Simons, pers. comm., Vleck, Vleck, Rahn and Paganelli, pers. comm., Flint and Whittow, unpubl. data, Grant, Whittow and Pettit, unpubl. data, Pettit and Whittow, unpubl. data, Whittow, Garnett and Teebaki, unpubl. data, Whittow, Pettit, Ackerman and Paganelli, unpubl. data.

mass. However, when incubation time was taken into account, predicted values (right-hand column of Table 13) were much closer to measured water loss. Accurate measurements of water loss were available only for two species nesting outside the tropics, Fork-tailed Storm-Petrel and Leach's Storm-Petrel. In both species, the predicted value based on fresh-egg mass and incubation time was again closer to measured rate than was the prediction based on fresh-egg mass alone. Similar conclusions may be made with regard to tropical Charadriiformes (Table 13). In Sooty Terns, there was little difference between measured values and either predicted value. However, in this species, incubation was not prolonged (Fig. 14). In Cassin's Auklets and the Common Puffins, two alcids breeding in higher latitudes, which had relatively long incubation periods (Fig. 14), the measured daily water loss from eggs was lower than predicted values but it was most closely approximated by predictions incorporating incubation period. In tropical Pelecaniformes also, the discrepancy between measured values and values predicted were attenuated by making allowance for incubation period (Table 13). In general, then, the divergence of measured rates of water loss for tropical seabirds from the value for birds in general can be attributed to prolonged incubation. However, there are sufficient discrepancies in the data (e.g., Wedge-tailed Shearwater, Great Frigatebird) to suggest that other factors may be involved in some instances.

The departure of water-vapor conductance of the eggshell of tropical seabirds from predictions based on fresh-egg mass may also be examined in terms of the contribution of prolonged incubation to this departure. Thus, Hoyt (1980) reported a relationship between incubation time (*I*), fresh-egg mass (*W*) and shell water-vapor conductance (G_{H_2O}):

$$G_{H_2O} = 2.32 \frac{W^{0.976}}{I^{0.73}}$$

(mg/day · torr) (g/day)

Data in Table 14 make it clear that, on the whole, measured water-vapor conductance of tropical Procellariiformes could be predicted with greater precision if incubation period was taken into account. This is also true for Fork-tailed Storm-Petrels and Leach's Storm-Petrels, two species nesting outside the tropics. A similar conclusion may be made with regard to tropical Charadriiformes (Table 14), and also for three alcids which breed in higher latitudes and which have long incubation periods (Fig. 14). In the four species of tropical Pelecaniformes included in Table 14, measured values of G_{H_2O} were closer to predic-

TABLE 13
COMPARISON OF THE MEASURED DAILY RATE OF WATER LOSS FROM THE EGG (\dot{M}_{H_2O}) WITH PREDICTED VALUES BASED ON THE MASS OF THE FRESHLY LAID EGG AND ON BOTH FRESH-EGG MASS (W) AND INCUBATION TIME (I), IN TROPICAL SEABIRDS

Order Species	Measured	\dot{M}_{H_2O} (mg/day) Predicted	
		$\dot{M}_{H_2O} = 13.243 W^{0.754^a}$	$\dot{M}_{H_2O} = 130.4 (W^{0.977}/I^{0.937})^a$
Procellariiformes			
Bulwer's Petrel (<i>Bulweria bulwerii</i>)	77	132	76
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	110	212	124
Christmas Shearwater (<i>Puffinus nativitatis</i>)	119	233	128
Phoenix Petrel (<i>Pterodroma alba</i>)	123	271	158
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	155	290	198
Dark-rumped Petrel (<i>Pterodroma phaeopygia</i>)	286	351	213
Laysan Albatross (<i>Diomedea immutabilis</i>)	674	939	651
Black-footed Albatross (<i>Diomedea nigripes</i>)	707	989	688
Charadriiformes			
White Tern (<i>Gygis alba</i>)	74	133	91
	79	142	100
Black Noddy (<i>Anous tenuirostris</i>)	106	144	103
Gray-backed Tern (<i>Sterna lunata</i>)	107	166	142
Sooty Tern (<i>Sterna fuscata</i>)	190	196	185
Brown Noddy (<i>Anous stolidus</i>)	150	209	162
Pelecaniformes			
Red-footed Booby (<i>Sula sula</i>)	167	284	196
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	199	332	245
Great Frigatebird (<i>Fregata minor</i>)	194	391	245

^a Ar and Rahn 1980. References for data on fresh-egg mass, incubation time, and water loss are given in the legends for Figures 1, 2, and 14, and Table 1.

tions based on fresh-egg mass and incubation than to values predicted solely on the basis of the fresh-egg mass alone.

The analysis performed in the preceding sections, for \dot{M}_{H_2O} and G_{H_2O} , may be extended to the functional pore area, A_p , and the number of pores, N . Thus Ar and Rahn (1978) established the following relationship between A_p , incubation time (I), fresh-egg mass (W), and shell thickness (L):

$$A_p = \frac{(2.2 WL)}{I} \text{ (mm}^2\text{) (g} \cdot \text{mm/day)}$$

In tropical Procellariiformes, and also in the two species from higher latitudes, predictions that took into account incubation time were a closer approximation to calculated values than were those based on fresh-egg mass alone (Table 15), again with the exception of the two larger species, the albatross. With regard to the tropical Charadriiformes remarks similar to those made above are applicable, viz. that predictions incorporating incubation period were not consistently superior to those that did not (Table 15). The func-

tional pore area of tropical Pelecaniformes was best approximated by the equation of Ar and Rahn (1978) in all four cases (Table 15).

It is apparent from Figure 9 that the number of pores in eggshells of all species included, with the exception of the two albatross, is less than predicted by Tullett and Board (1977) on basis of fresh-egg mass. Rahn and Ar's (1980) predictive equation (Table 16), incorporating incubation period, provided a better approximation of measured values for Procellariiformes, including Leach's Storm-Petrel, the only species from higher latitudes for which data are available. The combined use of incubation time and fresh-egg mass also provided a better estimate of the number of pores in shells of three tropical Pelecaniformes, than did fresh-egg mass alone (Table 16). In the Gray-backed Tern, a tropical species, the measured number of pores was closely approximated by the predicted value based on both fresh-egg mass and incubation. In Cassin's Auklet, from higher latitudes, a much closer approximation to measured values was furnished when incubation time was taken into account.

Hoyt and Rahn (1980) presented equations relating embryonic oxygen consumption prior to internal pipping to fresh-egg mass and also to

TABLE 14
COMPARISON OF THE MEASURED WATER-VAPOR CONDUCTANCE OF THE EGGSHELL (G_{H_2O}) IN TROPICAL SEABIRDS,
WITH PREDICTED VALUES

Order Species	Measured	G_{H_2O} (mg/torr·day) Predicted	
		$G_{H_2O} = 0.384W^{0.8148bc}$	$G_{H_2O} = \frac{2.32(W^{0.978}/I^{0.73})^{bc.de}}$
Procellariiformes			
Bulwer's Petrel (<i>Bulweria bulwerii</i>)	2.5	4.6	2.9
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	5.2	7.7	4.9
Christmas Shearwater (<i>Puffinus nativitatis</i>)	4.8	8.5	5.2
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	6.1	10.8	7.1
Dark-rumped Petrel (<i>Pterodroma phaeopygia</i>)	8.8	13.2	8.6
Laysan Albatross (<i>Diomedea immutabilis</i>)	32.0	38.2	27.4
Black-footed Albatross (<i>Diomedea nigripes</i>)	32.5	40.4	29.0
Charadriiformes			
White Tern (<i>Gygis alba</i>)	3.5	4.7	3.4
	2.5	5.0	3.7
Black Noddy (<i>Anous tenuirostris</i>)	4.5	5.1	3.8
Gray-backed Tern (<i>Sterna lunata</i>)	4.5	5.9	5.1
Sooty Tern (<i>Sterna fuscata</i>)	6.8	7.1	6.6
Brown Noddy (<i>Anous stolidus</i>)	7.0	7.6	6.0
Pelecaniformes			
Red-footed Booby (<i>Sula sula</i>)	5.8	10.5	7.6
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	9.0	12.4	9.5
Brown Booby (<i>Sula leucogaster</i>)	7.6	11.9	8.8
Great Frigatebird (<i>Fregata minor</i>)	7.5	14.8	10.0

^a Ar and Rahn 1978.
^b W = fresh-egg mass.
^c Hoyt 1980.
^d I = incubation period.
^e References for data on W , I and G_{H_2O} are given in Table 2 and Figures 3 and 4.

both fresh-egg mass and incubation time. Reservations were expressed in an earlier section regarding these equations because the equations were based on eggs in which the sequence of events during pipping varied. With these reservations in mind, values have been collected together in Table 17 to allow comparisons between the measured values for pre-internal pipping \dot{V}_{O_2} and predictions based on fresh-egg mass and incubation time. The purpose of this exercise was to test the conclusion, made earlier, that pre-pipping embryonic oxygen consumption of tropical seabirds was relatively low and, further, to determine whether this could be attributed to their prolonged incubation. In four tropical Procellariiformes, measured \dot{V}_{O_2} could be predicted with greater precision by the equation:

$$\dot{V}_{O_2} = 139 \frac{W^{0.85}}{I^{0.65}}$$

(ml/day) (g/day)

This was not the case for two petrels (Fork-tailed Storm-Petrel and Leach's Storm-Petrel) from higher latitudes. However, there are uncertainties regarding both incubation period (because of

egg neglect) and the precise point in incubation at which \dot{V}_{O_2} was measured in the Fork-tailed Storm-Petrel. In three tropical terns the predicted \dot{V}_{O_2} was considerably closer to the measured value when corrected for incubation time (Table 17).

Hoyt and Rahn (1980) assembled evidence to show that the total amount of oxygen required by the embryo over the entire incubation period averaged 102 ml/g egg. They claimed this value was independent of incubation time. In Table 18 a number of seabirds are ranked according to the degree to which their incubation times exceed predictions based on fresh-egg mass. In Procellariiformes it was clear that the amount of oxygen consumed per gram of fresh-egg mass greatly exceeded Hoyt and Rahn's (1980) prediction, particularly in smaller species with relatively long incubation periods. This trend was not apparent in Charadriiformes. A similar conclusion was made by Vleck et al. (1980) with regard to Procellariiformes. Ackerman (1981) presented a predictive equation for total oxygen consumed by an avian egg, predicated on the belief that an increase in either egg mass or incubation time incurs an increase in oxygen requirements. In

TABLE 15
COMPARISON OF THE FUNCTIONAL PORE AREA OF THE SHELL (A_p), CALCULATED FROM THE WATER-VAPOR CONDUCTANCE (G_{H_2O}) AND SHELL THICKNESS (L), WITH PREDICTED VALUES BASED ON THE MASS OF THE FRESHLY-LAID EGG (W) AND INCUBATION PERIOD (I), IN TROPICAL SEABIRDS^a

Order Species	Calculated ^b	A_p (mm ²) Predicted	
		$A_p = 9.2 \cdot 10^{-3} \cdot W^{1.2365}$ ^c	$A_p = 2.2WL/I^d$
Procellariiformes			
Bulwer's Petrel (<i>Bulweria bulwerii</i>)	0.21	0.40	0.21
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	0.42	0.87	0.32
Christmas Shearwater (<i>Puffinus nativitatis</i>)	0.55	1.01	0.49
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	0.71	1.45	0.69
Dark-rumped Petrel (<i>Pterodroma phaeopygia</i>)	0.95	1.98	0.78
Laysan Albatross (<i>Diomedea immutabilis</i>)	7.02	9.94	4.72
Black-footed Albatross (<i>Diomedea nigripes</i>)	7.73	10.82	5.39
Charadriiformes			
White Tern (<i>Gygis alba</i>)	0.26	0.41	0.22
	0.20	0.45	0.26
Black Noddy (<i>Anous tenuirostris</i>)	0.38	0.46	0.28
Gray-backed Tern (<i>Sterna lunata</i>)	0.48	0.58	0.44
Sooty Tern (<i>Sterna fuscata</i>)	0.69	0.76	0.63
Brown Noddy (<i>Anous stolidus</i>)	0.72	0.85	0.55
Pelecaniformes			
Red-footed Booby (<i>Sula sula</i>)	0.99	1.40	1.14
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	1.30	1.80	1.22
Brown Booby (<i>Sula leucogaster</i>)	1.33	1.68	1.29
Great Frigatebird (<i>Fregata minor</i>)	1.18	2.36	1.31

^a References for data on W , I and A_p are given in Table 4 and Figures 7 and 8.

^b Rahn et al. 1976.

^c Ar et al. 1974.

^d Ar and Rahn 1978.

TABLE 16
COMPARISON OF THE MEASURED NUMBER OF PORES IN THE EGG SHELLS (N) OF TROPICAL SEABIRDS WITH PREDICTED VALUES^a

Order Species	N (pores/egg)		
	Measured	Predicted	
		$N = 1449W^{0.42}$ ^b	$N = 3390(W/I)^{0.96}$ ^c
Procellariiformes			
Bulwer's Petrel (<i>Bulweria bulwerii</i>)	2439	5215	1712
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	4159	6786	2773
Phoenix Petrel (<i>Pterodroma alba</i>)	3798	7795	3509
White-tailed Shearwater (<i>Puffinus pacificus</i>)	3587	8089	3889
Dark-rumped Petrel (<i>Pterodroma phaeopygia</i>)	4553	8992	4694
Laysan Albatross (<i>Diomedea immutabilis</i>)	15,753	15,563	14,011
Black-footed Albatross (<i>Diomedea nigripes</i>)	16,700	16,013	14,736
Charadriiformes			
Gray-backed Tern (<i>Sterna lunata</i>)	3165	5934	3217
Pelecaniformes			
Red-footed Booby (<i>Sula sula</i>)	5778	7992	4347
Red-tailed Tropicbird (<i>Phaethon rubricauda</i>)	4536	8712	5434
Great Frigatebird (<i>Fregata minor</i>)	5368	9548	5385

^a W = fresh-egg mass; I = incubation period.

^b Tullett and Board 1977.

^c Rahn and Ar 1980.

TABLE 17
COMPARISON OF THE EMBRYONIC OXYGEN CONSUMPTION (\dot{V}_{O_2}), MEASURED IMMEDIATELY PRIOR TO THE INITIAL EVENT DURING PIPPING, WITH PREDICTED VALUES^a

Order Species	Measured	\dot{V}_{O_2} (ml/day)	
		Predicted	
		$\dot{V}_{O_2} = 28.9W^{0.714b}$	$\dot{V}_{O_2} = 139(W^{0.85}/I^{0.65})^b$
Procellariiformes			
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	246	399	253
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	305	538	346
Laysan Albatross (<i>Diomedea immutabilis</i>)	1250	1636	1125
Black-footed Albatross (<i>Diomedea nigripes</i>)	1225	1717	1182
Charadriiformes			
White Tern (<i>Gygis alba</i>)	159	274	198
Black Noddy (<i>Anous tenuirostris</i>)	184	344	211
Brown Noddy (<i>Anous stolidus</i>)	283	403	312

^a W = fresh-egg mass; I = incubation period. References for data on W , I and \dot{V}_{O_2} are given in Table 8.

^b Hoyt and Rahn 1980.

Table 19 the measured total volume of oxygen is compared with Ackerman's prediction derived from fresh-egg mass and incubation time. Allowing for variation in incubation time of the Fork-tailed Storm-Petrel, the small number of experimental observations on which oxygen consumption is based in some instances, and on other sources of variation and error, Ackerman's

equation provides a reasonably good estimate of oxygen consumption of the embryo.

The overall conclusion to be drawn from this discussion is that many of the differences between tropical seabirds and seabirds from higher latitudes, with regard to gas transfer between the egg and its environment, may be attributed to the prolonged incubation prevalent in tropical

TABLE 18
TOTAL VOLUME OF OXYGEN ($V_{O_2, tot}$, ml) CONSUMED BY THE EMBRYO (PER GRAM OF FRESH-EGG MASS) IN SEABIRDS RANKED ACCORDING TO THE DEGREE TO WHICH INCUBATION IS PROLONGED

Order Species	I_m/I_p^a	$V_{O_2, tot}/g_{egg}$	Reference
Procellariiformes			
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>)	2.1	179	Rahn and Huntington, pers. comm.
Fork-tailed Storm-Petrel (<i>Oceanodroma furcata</i>)	1.9	208	Vleck and Kenagy 1980
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	1.8	143	Pettit et al. 1982b
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	1.8	133	Ackerman et al. 1980
Laysan Albatross (<i>Diomedea immutabilis</i>)	1.6	104	Pettit et al. 1982a
Black-footed Albatross (<i>Diomedea nigripes</i>)	1.6	99	Pettit et al. 1982a
Charadriiformes			
White Tern (<i>Gygis alba</i>)	1.5	110	Pettit et al. 1981
Black Noddy (<i>Anous tenuirostris</i>)	1.4	128	Pettit and Whittow, unpubl. data
Brown Noddy (<i>Anous stolidus</i>)	1.4	119	Pettit and Whittow, unpubl. data
Common Tern (<i>Sterna hirundo</i>)	1.0	78	Rahn et al. 1974
Herring Gull (<i>Larus argentatus</i>)	0.8	110	Rahn et al. 1974
		129	Drent 1970

^a I_m = measured incubation time; I_p = incubation time predicted by Rahn and Ar 1974 ($I = 12.03W^{217}$).

TABLE 19
TOTAL VOLUME OF OXYGEN ($V_{O_2, tot}$) CONSUMED BY THE EMBRYOS OF SEABIRDS^a

Order Species	$V_{O_2, tot}$ (ml)		Measured/ predicted
	Measured	Predicted ^b	
Procellariiformes			
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>)	1881	1472	1.3
Fork-tailed Storm-Petrel (<i>Oceanodroma furcata</i>)	2831	2018 ^c	1.4
Bonin Petrel (<i>Pterodroma hypoleuca</i>)	5606	4890	1.1
Wedge-tailed Shearwater (<i>Puffinus pacificus</i>)	7980	7281	1.1
Laysan Albatross (<i>Diomedea immutabilis</i>)	29,619	30,930	1.0
Black-footed Albatross (<i>Diomedea nigripes</i>)	30,185	33,060	0.9
Charadriiformes			
White Tern (<i>Gygis alba</i>)	2563	2641	1.0
Black Noddy (<i>Anous tenuirostris</i>)	3174	3910	0.8
Brown Noddy (<i>Anous stolidus</i>)	4772	4196	1.1
Common Tern (<i>Sterna hirundo</i>)	1599	1865	0.9
Herring Gull (<i>Larus argentatus</i>)	9933	7186	1.4

^a For sources of information see Table 18.

^b Ackerman 1981.

^c For "average" incubation time of 50 days.

seabirds. Differences within the tropical seabird community are also explicable, to some extent, in terms of duration of incubation. Furthermore, in Procellariiformes, which have the longest incubation periods, quantitative differences between eggs of different species seem to be more closely related to the degree to which their incubation is prolonged rather than to their geographical distribution.

Prolonged incubation has clearly necessitated substantial adaptive changes in the physiology of eggs and embryos. Nevertheless, it is equally true to conclude that other factors have played a part in shaping incubation characteristics of tropical seabirds. Ironically, we shall have a better understanding of these factors when we know more about incubation physiology of seabirds breeding outside the tropics.

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